

**STUDIES
ON SCHOENUS VEGETATION
IN SOUTH AND SOUTHEAST
SWEDEN**

CARIN TYLER
DEPARTMENT OF PLANT ECOLOGY
UNIVERSITY OF LUND, SWEDEN
LUND 1979



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Carin Tyler
Fil. mag., Ld

Bye due permission of the Faculty of Science of the
University of Lund to be publicly defended at the
Department of Plant Ecology on October 1, 1979, at
10⁰⁰ a.m., for the degree of Filosofie Doktor.

In Memorial of my father, Fil. Dr. h.c. Per Benander,
Höör, and my uncle, President of the local government
comitee Håkan Nilsson, Benestad, who both have given
me the spiritual aid, patience and courage to accom-
plish this work



The dissertation is based on the following papers:

- I. Classification of *Schoenus* communities in South and Southeast Sweden.
- II. *Schoenus* vegetation and environmental conditions in South and Southeast Sweden.
- III. Soil acidity and distribution of species on tussocks and interspaces in *Schoenus* vegetation of South and Southeast Sweden.

The papers are referred to as I, II, and III, respectively.

INTRODUCTION

Due to the occurrences of orchids and other rare species the Swedish rich fens and extremely rich fens (Du Rietz 1949) have attracted much attention from botanists. Numerous articles with descriptions of the flora of such fens are published in popular magazines and scientific journals. However, all these affectionate studies have one deficiency in common: they cannot be used for comparisons either in time or in space, because they are incomplete with regard to both qualitative and quantitative species data. This is a serious lack, because complete vegetation analyses are few (I) and there is a great demand of information about both former and present vegetation of these fens as a basis for protection and management considerations. The rich fens have suffered seriously from the activities in the present day community. They occupy a diminishing area and are often in a state of rapid alteration. Knowledge about the rich fen vegetation of a region is necessary if the best (least altered) fens are to be selected for protection. Knowledge about the developmental changes and (if possible) their causes are necessary if such changes are to be discovered and brought to a standstill at an early stage.

In this study only one type of extremely rich fen vegetation is considered, the *Schoenus* phytocoenoses (sensu Westhoff & van der Maarel 1973). The term wetland is preferred because

many sites lack peat formation (I). The investigation area is restricted to provinces in South and South-east Sweden with occurrences of *Schoenus*. The aim of the study is to increase the knowledge about the regional differentiation of the *Schoenus* phytocoenoses, the probable successional changes, the differences in species distribution between tussocks and interspaces, some soil conditions, and the particular conditions which separate the sites of the different vegetation types (phytocoena, Westhoff & van der Maarel, 1973).

METHODS

Numerical methods (TABORD classification, ORDINA principal coordinate analysis and Reciprocal averaging, RA) have been of decisive importance to the analysis of the data. The result of the conventionally classification mainly agreed with the result obtained by the TABORD classification on the lowest threshold level. However, it remained to determine the group membership of several relevés with intermediate species composition and to distinguish the proper subdivisions. Numerical classification was preferred in this case not merely because it works fast, but particularly because it is an objective method giving similarities between groups of relevés in numerical values. It also points out the most important species.

At the time when the author had to decide the most proper ordination technique the fight was hard between the advocates of mathematically simple and more elaborate techniques (Austin & Orloci 1966, Gauch & Whittaker 1972, Beals 1973). The reliability of most such techniques was sometimes questioned (Austin & Noy-Meir 1971, Groenewoud 1976), particularly because the techniques presuppose linearity in species response to environmental conditions. The technique of reciprocal averaging had been described recently (Hill 1973) and with calculations fairly easy to understand. It was considered

to lack the drawbacks of earlier techniques and to be applicable also to untransformed environmental data. It also gave auspicious results when tested on some of the present environmental data. Later, when some authors had examined the mathematical and biological consequences of most ordination techniques and also of data transformations and data standardizations (Noy-Meir 1973, Noy-Meir et al. 1975, Austin 1976, Gauch et al. 1977), RA was found to be as imperfect as other techniques in common use. However, properly understood and applied, all ordination techniques are fully applicable in approximating the interrelations between species, environmental variables or both.

The possibility of ordinating species and environmental data in a common vegetational space (Beals 1973), i.e. an 'ecosystematic' ordination (Jeglum et al. 1971), especially attracted the present author, though some important objections to such ordinations may be raised. The influence on the ordination result of a larger number of species than of environmental variables and the importance of environmental variables not measured for the vegetational gradients are conditions which must be taken under consideration. Thus it did not seem advisable to use only 'ecosystematic' ordination. However, the combination of species, environmental and 'ecosystematic' ordination seemed to be a feasible way of analysis. It was observed that RA excellently solved the task to elucidate both species gradients, environmental gradients and the relations between them. It also gave the best possible information about the distribution of species on tussocks and interspaces.

VEGETATION

The TABORD classification resulted in a hierarchial system of phytocoena (Fig. 2, I), each characterized by a certain species composition. Character species, i.e. species confined to only one phytocoenon are lacking, except for *Euphrasia saliburgensis* which is parasiting on only *Schoenus ferrugineus* in the province of Gotland (Pettersson 1958). The *Schoenus*

species are always considered character species of phytocoena in which they occur (e.g., Görs 1964). All other species are present also in other phytocoena of extremely rich fens, of poor fens, of bogs, of calcareous fen meadows, or of wet meadows. Thus the associations are distinguished only by their characteristic species compositions. In table 2 (I) the species are arranged in groups according to their environmental preferences in order to make the long table more easy to read and facilitate the interpretation of the species composition of each phytocoenon.

The *Oxycoccus-Schoenus ferrugineus* association and the *Primula-Schoenus ferrugineus* association are separated by several differential species, i.e. *Oxycoccus quadripetalus*, *Myrica gale*, *Scirpus hudsonianus*, *Primula farinosa*, *Preissia quadrata*, *Parnassia palustris* and the groups of acidophilous or indifferent fen species and basophilous fen species (Table 2, I). The distribution areas are also different, the *Oxycoccus-Schoenus* association is confined mainly to the province of Uppland and *Primula-Schoenus* association to the other provinces.

Each association consists of several well-distinguished subdivisions, five in the *Oxycoccus-Schoenus* and seven in the *Primula-Schoenus* association. The *Sesleria* and the *Riccardia sinuata-Moerckia hibernica* phytocoena are representatives of the *Oxycoccus-Schoenus* association with occurrence on Gotland and Öland respectively. The *Utricularia-Drepanocladus* and *Selaginella-Pinus* phytocoena are supposed to represent different stages in the successional development from very wet to moist site conditions of the *Schoenus* phytocoenoses in Uppland.

The phytocoena of the *Primula-Schoenus ferrugineus* association are distributed on three groups, the *Sesleria*, the *Bartsia-Ophrys* and the *Valeriana* group. The *Sesleria* group, distinguished by the presence of *Sesleria coerulea* and members of the drier meadow species group comprises three phytocoena, in Uppland, Gotland and Öland respectively. In the

Tofieldia phytocoenon of Gotland *Tofieldia calyculata*, *Pinguicula alpina*, *Calamagrostis varia* and *Gymnadenia odoratissima* are differential species and the drier meadow species group belongs to the characteristic species composition. The drier meadow species group is also typical of the *Carex hostiana* phytocoenon, distributed on Öland. The similarities between these two phytocoena is further emphasised by the presence of *Juniperus communis*, and by the development towards *Sesleria* meadows, when grazing ceases. The third phytocoenon of the *Sesleria* group constitutes a transitional type between the *Primula*- and the *Oxycoccus-Schoenus ferrugineus* associations and is represented by a few sites investigated in Uppland.

Bartsia alpina and *Ophrys insectifera* are the very weak differential species of the *Bartsia-Ophrys* group, distributed in Östergötland, while *Valeriana dioica* is a good differential species of the *Valeriana* group with distribution in Skåne. Both these groups consist of each two phytocoena, a *Carex lepidocarpa* phytocoenon distinguished by spring fen species (*Bartsia-Ophrys* group) and a *Calliergonella* phytocoenon distinguished by drier meadow species (*Bartsia-Ophrys* group) and liverworts of acid peat (*Valeriana* group). A gradient of wet meadow species from the *Oxycoccus-Schoenus* association to the *Carex lepidocarpa* phytocoenon of the *Valeriana* group can be distinguished. A development towards *Molinia* wet meadows of the *Calliergonella* phytocoena are probable.

In addition to these two associations the classification resulted in five phytocoena which are regarded as nuclei of an association. Two phytocoena with occurrences of sea-shore species, a *Glaux-Schoenus ferrugineus* and a *Glaux-Schoenus nigricans* phytocoenon, were distinguished. These phytocoena occur on Öland and Gotland, respectively. A *Cladium-Schoenus nigricans* phytocoenon with several swamp species occurs as a transitional zone between *Cladium* swamps and *Schoenus ferrugineus* wetlands on Gotland. The species composition of the *Schoenus intermedius-Schoenus ferrugineus* phytocoenon is rather similar to that of the *Primula-Schoenus* association.

The few high-tussocky *Schoenus nigricans* phytocoenoses in Skåne belong to the *Fissidens osmundoides*-*Schoenus nigricans* phytocoenon, characterized by *Fissidens osmundoides*, *Calypogeia fissa*, and *Cephalozia connivens*. These *Schoenus* tussocks are assumed to be open to invasion by more acidophilous species later resulting in the disappearance of *Schoenus*.

The species pattern is studied also by the ordination techniques ORDINA and RA (II). These techniques gave similar results with regard to stand ordinations and species gradients. The distribution of the stands within each phytocoenon is best demonstrated by ORDINA (Fig. 11A, II), while the relations between phytocoena are interpreted more easily in the planes obtained by RA. A sequence of phytocoena: *Utricularia*-*Drepanocladus* — *Selaginella*-*Pinus* — *Riccardia*-*Moerckia* — *Calliergonella* — *Carex lepidocarpa* — *Sesleria* group — *Schoenus intermedius*-*Schoenus ferrugineus*/*Cladium*-*Schoenus nigricans* — *Glaux*-*Schoenus nigricans*, is distinguished in Fig. 11C (II).

Distribution of species on tussocks and interspaces

The bryophyte sequence: *Scorpidium* - *Drepanocladus* - *Campylium* - *Tomenthypnum* - *Sphagnum fuscum*, stated by Du Rietz (1949), was reconfirmed for Uppland by use of belt transects extended over *Schoenus* tussocks and interspersed *Sphagnum* hummocks, and RA technique. Other bryophytes and vascular plants also proved to be unevenly distributed on tussocks, interspaces and hummocks, and a generalized sequence of species was obtained (table 1, III). The bryophyte sequence *Scorpidium* - *Drepanocladus*/*Campylium* - *Ctenidium*, *Fissidens*, described by, e.g. Malmer (1965) may be reconfirmed for Öland but was not detectable in Östergötland and Skåne. In these two provinces *Ctenidium molluscum* is distributed on both tussocks and interspaces in most transects studied and bryophyte sequences common to all transects cannot be demonstrated. In Östergötland each transect has its own species composition and in most transects different species occur on tussocks and in interspaces. Successional development and/or soil and moisture conditions typical of these sloping

fens are assumed to be the reasons for the lack of common bryophyte sequences. However, some bryophytes and vascular plants are in all transects, where they appear, distributed either on tussocks or in interspaces. *Potentilla erecta*, *Cephalozia* and *Calypogeia* species and *Ditrichum flexicaule* occur on the top of the tussocks. *Campylium elodes* and *Preissia quadrata* are mostly distributed on intermediate levels, and *Cratoneuron commutatum*, *Riccardia pinguis*, *Juncus* and *Eriophorum* species in the interspaces.

ENVIRONMENT

Each phytocoenon is environmentally characterized in table 2 (II). Great differences between them are demonstrated, especially in 'peat'-thickness, pH, C:N, Ca:Mg, content of organic carbon, carbonate and available phosphate. Two groups are obtained, when all normally distributed environmental variables are correlated. Within each group the variables are significantly positively correlated; between the groups negative correlations are obtained. The carbon grouping consists of 'peat'-thickness, content of water and organic carbon, and C:N, and the carbonate grouping of dry weight, pH, CEC, Ca, CO_3 , Ca:Mg, and N (Fig. 4, II). The variables of the carbon grouping are ordered in relation to degree of correlation on the one end of the first axis of all environmental ordinations (Table 1, II). No such 'correlation coefficient order' of the carbonate grouping is found on any axis. A first direction of variation, the carbon versus the carbonate grouping, is obtained by these first axes, and a second direction, available phosphate versus Ca:Mg, by the second axes, when phosphate is included in the ordination. The interrelations between species and environment are studied by inspection of species gradients and phytocoenon sequences in relation to field observations and known species preferences, by plotting environmental data on planes of stand ordinations, and by comparing species, environmental and ecosystemic ordinations. The interpre-

tation in an environmental context of species gradients and axes, obtained by species and stand ordinations, is not easy, because factor complexes rather than single factors seem to operate on the species distributions. A moisture factor complex seems to be related to the phytocoenon sequence mentioned above (p. 6). A drop in general soil water level is related to the *Utricularia-Drepanocladus* -- *Calliergonella* part, a drop in summer water level to the *Carex lepidocarpa* -- *Sesleria* part, and differences between land and sea-shore to the *Sesleria* group -- *Glaux-Schoenus nigricans* part of the sequence. However, a plot of environmental data studied on the pattern of stands obtained in the stand ordinations does not give any gradients (Fig. 7, II). On the other hand, a comparison of the different ordinations demonstrates the close relationship between environment and vegetation. The 'ecosystemic' ordination is almost the sum of the species and the environmental ordinations, in that the same arrangement of species and environmental variables is demonstrated by all these ordinations. The carbon grouping and the species typical of the *Oxycoccus-Schoenus* association are associated. The carbonate grouping is less homogeneous. High values of the variables of this grouping are associated with different species combinations (phytocoena): CO_3 and Ca:Mg with *Sesleria coerulea*, *Calamagrostis varia*, *Juniperus communis* (= *Tofieldia* and *Carex hostiana* phytocoena), and dry weight with *Schoenus intermedius-Schoenus ferrugineus* and *Glaux* phytocoena. A high content of available phosphate (non-normally distributed) is associated with a vegetation of *Valeriana dioica*, *Carex lepidocarpa* and *Juncus subnodulosus* (*Valeriana* group). Other phytocoena are related to intermediate values of the environmental variables (e.g. Fig. 12, II).

However, a high content of water and organic carbon, high C:N and deep 'peat' (= the carbon grouping) are soil properties developed under certain interactions between vegetation and hydrological conditions, and the hydrological conditions are considered the most important environmental factor complex for the differentiation of the *Schoenus* phytocoenoses, in accordance with the interpretation of species and stand ordi-

nations. Topogeneous, stagnant soil water and permanently high water table are assumed to give rise to site conditions typical of the *Oxycoccus-Schoenus* association, while only temporarily flooding, or flow of soligenous soil water rich in oxygen facilitates litter decomposition to such an extent that no real peat formation occurs. Temporarily flooded depressions with mainly topogeneous soil water and the precipitation of lake marl are the sites of phytocoenoses classified as representing the *Tofieldia* and *Carex hostiana* phytocoena (cf. Table 3, II). Soligenous soil water may also be rich in nutrient and cause the development of a more demanding vegetation, e.g. of the *Valeriana* group. The *Bartsia-Ophrys* phytocoenoses occur in sites with soligenous soil water and probably a permanently high water table.

Estimation of soil pH along the belt transects resulted in four types of pH gradients from low to high levels of the transects (Fig. 29, III). A linear relation and a pH amplitude of less than one pH unit are associated with occurrences of *Ctenidium molluscum* on all height levels and lack of zonated bryophyte distributions (Table 4, III). Inverse linear relation and a pH amplitude ≥ 2 units are also associated with the occurrence of *Ctenidium* on both tussocks and in interspaces, though other bryophytes often have restricted distributions. Curvilinear relations are typical of transects with distinct differences in bryophyte distributions. Scattered high pH-values at lower levels of the transect and scattered very low values at higher levels are associated with transects extending over both *Schoenus* tussocks and *Sphagnum* hummocks, the *Schoenus* phytocoenosis growing on peat with a high pH and the *Sphagnum rubellum* or *Sph. fuscum* phytocoenoses on acid peat.

ACKNOWLEDGEMENT

The study was financially supported by the University of Lund, Kungliga Fysiografiska Sällskapet, Lund, and the National Swedish Environment Protection Board within the project "Management of calcareous fen meadows and extremely rich fens in South Sweden". These supports are gratefully acknowledged.

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